LETTER TO THE EDITORS

Bees, White Flowers, and the Color Hexagon – A Reassessment? No, Not Yet

Comments on the contribution by Vorobyev et al.

L. Chittka
Thodor-Boveri-Institut für Biowissenschaften, Verhaltenphysiologie/Soziologie,
Am Hubland, D-97074 Würzburg, Germany
e-mail: chittka@biozentrum.uni-wuerzburg.de, Tel.: +49-931-8884321, Fax: +49-931-8884309

Received/Accepted: 3 September 1999

It is always easy to train them to a true color, but training to a white paper or cardboard is sometimes easy and sometimes quite difficult. She [Hertz] tested various white papers and found that some of them absorbed ultraviolet rays. To these papers the bees could be trained very easily. But other white papers reflected the ultraviolet, just as they did the rays visible to us. This white the bees ... could not learn to seek ... out with certainty ....

K. von Frisch (1950)

Optically neutral ... white flowers are rare exceptions in nature. Many will think that the failure of bees to memorize "white" as an appetitive stimulus is a consequence of the absence of pure white flowers. I, for my part ... am convinced that the neutral character of white has deeper physiological roots, and that, if there is a causal relationship between floral colors and the sensory functions of bees, then it is the bees that have dictated floral coloration. A thorough absorption of ultraviolet should be the most simple and therefore most widespread means available for plants, to generate an intensive colorfulness of floral parts.

M. Hertz (1938) [translation by L.C.]

In agreement with former findings, the colored stimuli were learned well and were easily discriminated from the background. The achromatic stimulus was not ... even after 40–50 learning trials, only 2 out of 19 bees were able to learn it. Moreover, these two bees were not consistent throughout the experiment ....

M. Giurfa et al. (1996)

The fact that many animals, such as bees, see the world in colors entirely differently from humans has long fascinated researchers. One of the most peculiar findings in bee color science is that training to UV-reflecting white targets on black or gray backgrounds is much harder than training them to colors which offer strong chromatic contrast to their background. As early as 1967, Menzel was able to list seven empirical studies to support this observation, some of which actually found that training bees to such white stimuli was impossible – even though for the human observer, such targets are highly conspicuous. These results may be due to a difficulty to *learn* "white" as predictors of reward, not a difficulty to *detect* it. In some reports, such as the one by Giurfa et al. (1996) cited above, detectability was likely the limiting factor. Hertz (1938), for example, described the flight behavior of bees, saying that they flew slowly and very close the ground, probing various places other than the location of the target, clearly indicating that they had difficulties detecting it. Decades before the now widespread use of *color spaces* for bees, Hertz conjectured that the rarity of UV-reflecting white flowers in nature is due to a physiological peculiarity of bee vision, although she did not yet specify what mechanisms might underlie this peculiarity. Later several workers found that when stimuli differ both in intensity and chromaticity, bees ignore the intensity differences or weigh them less heavily (Backhaus 1991). Backhaus (1991) and Chittka (1992) developed color opponent spaces for bees, whose metrics would predict this phenomenon. These spaces are two-dimensional and do not include a brightness dimension; therefore stimuli which differ merely in intensity fall into the same location and are predicted to be hard to distinguish (but see Backhaus 1992 for exceptions). Both of these models provide a physiological explanation, which Hertz lacked: if bees code color without a brightness dimension, green foliage and UV-reflecting white flowers are predicted to be similar. This is because green leaves (unlike green monochromatic lights) are relatively achromatic for bees, as a consequence of their reflectance function which increases smoothly from shorter to longer wavelengths, and the fact that the bees' color receptors decrease in relative sensitivity from shorter to longer wavelengths (Chittka et al. 1994). This prediction dates back to Daumer (1958) and is qualitatively independent of the particular color space used.

Based on a survey of 1063 flower colors, Chittka et al. (1994) supported Hertz's observation of the near absence of UV-reflecting white flowers. One might assume that the rarity of such coloration is caused by phylogenetic or pigment constraints. A possible way out of this ambiguity is to look at mutant plants whose flowers differ only in pigmentation, not in reward or other floral traits. Indeed, Glover and Martin (1998) have recently shown that white UV-reflecting snapdragon (*Anthirrhinum majus*) mutants set fewer seeds than UV-absorbing ones. Thus the evidence from modeling, ecology, and empirical data seemed to fit together snugly like the pieces of a puzzle.

Sometimes, however, taking a closer look at a classical story can reveal unexpected gaps in our knowledge. This is exactly the approach taken by Vorobyev et al. in the accompanying article in this issue. They point out that our evidence for the supposed similarity between green foliage and white UV-reflecting flowers is only indirect; no one has actually tested just how hard it is for bees to detect such white targets bees when presented on a *green* background. In a similar setup Giurfa et al. (1996) previously tested a UV-reflecting bright stimulus on a gray background. The results of this test are quoted verbatim above: bees appear to have immense difficulty in detecting this target presented on a gray background. Hertz (1938) used black and gray backgrounds. However, we were still lacking data for similar stimuli presented on a green, foliage-type background. Vorobyev et al. have started to fill this lacuna, and in fact they managed to train three bees to accomplish the task. On the basis of these findings, Vorobyev et al. suggest abandoning the hypothesis that white flowers are rare because they are hard to detect and discontinuing the use of the color hexagon.

I believe caution is warranted before we adopt such drastic measures. First, Vorobyev et al. trained bees to a white, UV-reflecting stimulus which is unlike the ones used by other authors and wholly unlike those of white, UV-reflecting flowers. Their target was an "ideal" white which reflects uniformly across the bee visual spectrum with 95% reflectance. White, UV-reflecting flowers commonly reflect all light above 360 nm and absorb at wavelengths below this value, whereas the reflectance boundary of UV-absorbing white flowers is roughly at 410 nm. In such flowers reflectance rarely exceeds 60%. The new result would be more relevant had Vorobyev et al. used a target which is more similar to reflectance spectra of natural flowers. Second, it is not fully satisfactory to show that bees can solve the task. Few scientists have claimed that it is *impossible* to train bees to white. It would be useful to have some measure of *quality* of performance, such as times taken to detect the target, or the shape of the learning curve; after extensive training, bees might be able to use cues that they do not naturally use. Once such paradigms are available, the most relevant comparison would be to compare performance on UV-reflecting vs. absorbing white flowers. This experiment remains to be carried out. *Some* white stimuli clearly appear to be hard to detect on *some* backgrounds, as shown by earlier work, and surely this new finding cannot nullify the older ones. Thus a reconciliation of the old and the new findings would be more satisfactory than a polarized debate. I advocate carrying out a study by systematically varying both background and target to determine the way in which color distance affects detectability, and which color space most accurately predicts it.

It appears to me that the color hexagon is attacked too harshly by Vorobyev et al. The reasons are unclear, because the "white flower hypothesis" predates the color hexagon by several decades. More importantly, other color spaces currently available for bees are similar in one aspect: they lack a brightness dimension, and therefore UV-reflecting white flowers are predicted to be more similar to green foliage than are UV-absorbing white flowers. For example, Vorobyev and Brandt (1997; their Fig. 6) plotted examples of both flower types in the color triangle and showed that UV-absorbing *Calystegia sepium* flowers have more than twice the color distance to green leaves than do UV-reflecting *Allium neapolitanum* flowers. This also shows that the similarity of UV-reflecting white flowers and green foliage is not due to the nonlinear transduction function of the photoreceptors, which is one of the foundations of the color hexagon (but not the color triangle). Vorobyev et al. claim that the color hexagon inadequately predicts better discriminability of stimuli near background intensity as a result of this nonlinear transduction. Such transduction functions, however, are well supported by receptor physiology (Lipetz 1979) and, more importantly, have been shown to be relevant in bee color discrimination (Backhaus 1992). In fact, Backhaus observed just the saturation effect that Vorobyev et al. claim is an artefact of the color hexagon. Thus the color space designed by Backhaus (1991) makes exactly the same prediction for white flowers and green foliage as the color hexagon, and Backhaus' model has been used extensively by the authors (Giurfa et al. 1996; Vorobyev and Brandt 1997).

Finally, the *photon-noise limited color opponent model* indeed predicts that white is well distinguishable from a green backdrop, but it cannot explain the data from a third experiment which, unfortunately, the authors do not include in the present paper. They also found that bees are able to detect white targets on a gray background, for which the photon-noise limited model predicts the poorest detectability (M. Vorobyev, personal communication). Thus *all* models of bee color vision are in disagreement with the new results. This should not cause us to abandon these color spaces, or even any one of them. After all, the color hexagon owes its success to the fact that it predicts many behavioral and ecological data very well. Human color research teaches us that it is very hard to design a color space that accounts for color discrimination equally well in all areas of color space, under various intensity and illumination conditions, etc. One color space may appear best in one experimental paradigm, and another in a different one. Thus, even after many decades of human color research, the search for a universally applicable color space still resembles the search for the "Holy Grail", so that there are many different color spaces for humans on offer (Wyszecki and Stiles 1982). This should teach us that the path to an ideal color space for bees may not be smooth, but perhaps it can also teach us that we should drop all sense of dogma and pull "on the same end of the rope". Evolutionary ecologists, who need color spaces as tools to make predictions about real-life biology of their animals, will certainly be thankful if we accomplish this task.

Backhaus W (1991) Color opponent coding in the visual system of the honeybee. Vision Res 31:1381–1397

Backhaus W (1992) The Bezold-Brücke effect in the color vision system of the honeybee. Vision Res 32:1425–1431

Chittka L (1992) The color hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. J Comp Physiol [A] 170:533–543

Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. Vision Res 34:1489–1508

Daumer K (1958) Blumenfarben, wie sie die Bienen sehen. Z Vergl Physiol 41:49–110

Frisch K v (1950) Bees – their vision, chemical senses, and language. Cornell University Press, Ithaca

Giurfa M, Vorobyev P, Kevan P, Menzel R (1996) Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. J Comp Physiol [A] 178:699–709

Glover BJ, Martin C (1998) The role of petal cell shape and pigmentation in pollination success in *Antirrhinum majus*. Heredity 80:778–784

Hertz M (1938) Zur Technik und Methode der Bienenversuche mit Farbpapieren und Glasfiltern. Z Vergl Physiol 25:239–250

Lipetz LE (1971) The relation of physiological and psychological aspects of sensory intensity. In: Loewenstein WR (ed) Handbook of sensory physiology. Springer, Berlin Heidelberg New York, pp 192–225

Menzel R (1967) Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene (*Apis mellifica*). Z Vergl Physiol 56:22–62

Vorobyev M, Brandt R (1997) How do insect pollinators discriminate colours? Isr J Plant Sci 45:103–113

Wyszecki G, Stiles WS (1982) Color science: concepts and methods, quantitative data and formulae. Wiley, New York